Charles University
Faculty of Science

Study Programme: Biology

Branch of Study: Ecology and Evolutionary Biology

Miroslav Petruf

Niche Partitioning in Tropical Birds
Mechanizmy rozdelenia ník u tropických vtákov

Bachelor Thesis

Supervisor: RNDr. Ondřej Sedláček, Ph.D

Prague, 2017

Acknowledgement

I would like to thank my supervisor, RNDr. Ondřej Sedláček, Ph.D, for his time, support, and valuable suggestions that helped me shape this thesis. I am also thankful to my family and friends who have supported me throughout my studies.

Čestné prehlásenie

Čestne prehlasujem, že som túto prácu vypracoval samostatne, a všetky použité informačné zdroje a literatúru som riadne uviedol. Taktiež prehlasujem, že som túto bakalársku prácu, ani žiadnu jej časť, nepredložil na získanie iného alebo rovnakého akademického titulu.

V Prahe, 12. mája 2017 Podpis

Abstract in English

Niche partitioning is a process that allows species to coexist by minimizing competition. Niches get narrow with growing habitat heterogeneity, which is evident in tightly packed tropical communities. Closely related species exhibit a high niche overlap, which intensifies competition for resources in their sympatry. Such birds avoid competitive exclusion by foraging using different methods or in different strata. Character displacement makes sympatric species diverge in foraging niches as well as in morphology, allowing specialized species to access private resources. Tropical birds in seasonal environments tend to occupy different niches in the wet and in the dry season, based on the availability of resources in their preferred habitats. Resource subdivision in sympatric members of an ecological guild usually depends on body-size-determined dominance. Territoriality may depend on the costs and benefits of defending resources, which may change seasonally. Dominance statuses vary within populations of the same species, too, promoting intra-specific niche partitioning. Within-species differences in foraging can also be the result of sexual dimorphism or differences in reproductive roles. Moreover, intra-specific differences in foraging may also explain the partial migration of some tropical birds. The collected data about niche partitioning are key for improving conservation efforts in fragmented tropical habitats.

Keywords: niche differentiation; feeding ecology; specialization; habitat selection; phylogenetic structure; interspecific territoriality

Abstrakt v slovenčine

Rozdeľovanie ekologických ník umožňuje potenciálnym kompetítorom koexistovať. Niky sa s rastúcou heterogenitou habitatu zužujú, čo je zrejmé najmä v nahustených tropických spoločenstvách. Vysoký prekryv ník blízko príbuzných druhov zintenzívňuje kompetíciu o zdroje. Odlišným spôsobom zháňania potravy sa takéto vtáky dokážu vyhnúť kompetičnému vyčleneniu. V sympatrii môže dôjsť k posunu znakov, kedy sa druhy líšia nielen v potravnej nike, ale aj v morfológii. Špecializované druhy tak môžu využívať súkromné zdroje. Vtáky v sezónnom tropickom prostredí obsadzujú odlišné niky počas období vlhka a sucha kvôli kolísajúcemu množstvu zdrojov v preferovaných habitatoch. Dominantné postavenie sympatrických druhov v rámci ekologickej gildy je často odrazom ich telesnej veľkosti, a od toho sa odvíja aj to, ako sa podelia o zdroje. Teritorialita môže závisieť od nákladov a výhod obrany zdrojov, ktoré sa tiež môžu líšiť medzi sezónami. Dominantné postavenie je odlišné aj medzi jednotlivcami v rámci populácie, čo často viedie k vnútrodruhovému rozdeľovaniu ník. Navyše pohlavný dimorfizmus a rozdiely v reprodukčných rolách dokážu zapríčiniť odlišnosti v zháňaní potravy medzi pohlaviami. Vnútrodruhové rozdelenie ník môže taktiež slúžiť k vysvetleniu čiastočnej migrácie niektorých tropických vtákov. Dostupné poznatky o rozdeľovaní ník sú kľúčové pre zlepšenie ochranárskej práce vo fragmentovaných tropických biómoch.

Kľúčové slová: diferenciácia ník; potravná ekológia; špecializácia; biotopové preferencie, fylogenetická štruktúra; medzidruhová teritorialita

Contents

Introduction

The tropics hold the greatest diversity of avifauna on Earth, and there is no universal explanation as to why this is so (e.g. Klopfer and MacArthur 1960, Salisbury *et al.* 2012). The growing species diversity towards the equator is described by the latitudinal gradient of diversity (Stevens 1989, Gaston and Blackburn 1996), but its underlying mechanisms are not well understood (Salisbury *et al.* 2012).

Tropical latitudinal zones are generally deemed as stable in climate, or at least more stable than any other latitudinal zone (Janzen 1967, Hau *et al.* 2008). This should predict a constant availability of resources year-round. Nevertheless, the tropics exhibit seasonal shifts in precipitation, in the savannahs, for instance (Wright 2002), which causes resource scarcity and intensifies competition between and within species (e.g. Radford and du Plessis 2003). In the tropical rainforests, on the other hand, the dry season is short or completely absent (Primack and Corlett 2005), but the forest floor is usually dark and damp, which again limits plant growth. Species here are specialized for the unfluctuating temperatures, so even a 100m change in altitude may cause severe physiological stress (Janzen 1967). Tropical ecosystems are known for their patchiness (Bregman *et al.* 2015), and each patch has the potential to offer unique ecological niches for its residents to fill.

An ecological niche encompasses all the factors that influence an organism's fitness, and can also be understood as a specific role an organism plays in its environment, and this role is defined by the way the organism exploits that environment. The ecological niche can be divided into two kinds: fundamental niche and realized niche. The fundamental niche includes all the resources and factors of an organism's environment that can be exploited by it without being limited by competition. When we speak of the realized niche (also called actual), we incorporate competitive interference into the fundamental niche (Colwell and Futuyma 1971, Whittaker *et al.* 1973).

How species partition resources may reveal the ways in which potential competitors can coexist (Robertson *et al.* 2013). If sympatric competitors (i.e. those that co-occur) overlap in their niches and competition is high, both parties need to narrow down their niches to subdivide resources, or else the better competitor will exclude the other from the sympatry. Cody (1985) argues that similar parts of the same habitat may

be used by several species of birds, but perfect competitors (i.e. those who completely overlap in their ecological requirements, such as feeding, nesting and reproduction) cannot coexist (e.g. Hardin 1960, Diamond 1975, Colorado and Rodewald 2015, Rodríguez *et al.* 2015). Closely related birds are expected to have a high niche overlap (Bregman *et al.* 2015). Ecological requirements of a species are defined by the niche it occupies, and competition brings forward a potential for an ecological segregation (niche partitioning) in the shared environment, which minimizes competitive pressures (e.g. de Mendonça-Lima 2004). In other words, the term 'niche partitioning' is currently defined as differences in habitat and resource use (Mathias and Duca 2016).

Avoiding competition with sympatric species may be the main factor that drives species success, and this is shown in species abundance distributions, which are defined by the mean niche overlap of the species within an assemblage (Arellano *et al.* 2017). For this to happen, habitats must include microhabitats that can be exploited by specialized species, and the more heterogenous the habitats are, the more species they can carry (de Mendonça-Lima 2004). Naturally, their size must be in accordance to the species' minimal area requirements (Bregman *et al.* 2015).

Competition happens when con- or hetero-specific organisms exploit common resources that are in short supply (Birch 1957). Organisms compete in two ways; there is interference competition (i.e. direct competition, such as aggressive encounters) and exploitative (i.e. indirect competition via the exploitation of limiting factors, such as resources or space), and in general, ecologists consider competition to happen on an inter- or intra-specific level. The competitive exclusion principle (Gause 1934a) is fundamental to community ecology. For example, Terborgh and Weske (1975) found that at least two thirds of distributional limits in Andean birds are attributed to direct or diffuse competitive exclusion. Nonetheless, many examples of coexistence between closely related and/or similar species exist (e.g. Mendonça-Lima *et al.* 2004, Toyama and Saitoh 2011). Competition is not the only factor that limits species distributions (Terborgh 1971). Therefore, rather than assess the origins of their dramatic species-richness, the intention of my thesis is to summarize the hitherto collected data about niche differentiation among tropical birds, focusing mainly on food-niche differentiation in space and time, because once we know what resources are exploited within a community and by which species, we can determine a population's realized niche breadth, and the niche overlap within that population (Feinsinger 1976).

Interactions of species regulate biodiversity collapses (Bregman *et al.* 2015), and finely partitioned niches promote biodiversity due to constraints in dispersal (Salisbury *et al.* 2012). Therefore, studies focused on niche partitioning between species and the coexistence of species may be essential for conservation management, and almost all the articles discussed below highlight this.

The work is divided into two parts. First I intend to illustrate how species subdivide resources between each other, and then I discuss how conspecific tropical birds do the same within populations. Restricting the work to include birds from certain biomes only, such as savannahs or rainforests, would possibly result in the work being short due to a lack of available literature on niche partitioning in tropical birds (with the exception of climatic niches). Therefore, the only limitation this work has is its lack of examples from seabird communities.

Chapter I

Niche-Based Assessments of Coexistence: Food-Niche Partitioning between Species

In community ecology, one theoretical framework that aims to explain the processes which allow species to coexist in the same area can be found in community assembly (Colorado and Rodewald 2015). Diamond (1975) proposed a set of assembly rules by which he illustrated several filters that are imposed on a regional species pool, and how these filters limit the community structure and composition of local species. These rules have been deemed controversial, and only the basic predictions of Diamond's (1975) model have been confirmed thus far (Gotelli and McCabe 2002). Several studies have found evidence for at least some of them apply in specific cases, while others could not be confirmed yet (e.g. Gotelli and McCabe 2002, Colorado and Rodewald 2015).

Birds have been the most useful group for studying competition and niche partitioning (e.g. Colorado and Rodewald 2015, Mohd-Azlan *et al.* 2014, Salisbury *et al.* 2012), and comparing their food niches may pinpoint the factors of species' coexistence (Toyama and Saitoh 2011). The coexistence of phylogenetically related species is made possible by ecological niche segregation, which reduces competition in species with similar ecological requirements (e.g. Brown and Wilson 1956, Bulmer 1974, Abrams 1989, Grant and Grant 2006, De Léon *et al.* 2014).

The Coexistence of Congeneric Species

Assessing temporal segregation of niches and their overlap is a widely-used way to address the question of the coexistence of closely related species (De Léon *et al.* 2014). Closely related and/or ecologically similar species (i.e. those overlapping in their niche) are expected to exhibit the strongest interactions (e.g. Darwin 1859, Diamond 1975). In other words, birds of similar size, foraging behaviour and diet are most frequently involved in direct competition, and their co-occurrence is thus likely to be regulated on these axes (Bregman *et al.* 2015). This may result in communities with bigger dispersion in body or beak dimensions and/or foraging behaviour than expected by chance (i.e. overdispersion; e.g. MacArthur 1958, Lack 1971 in Bregman *et al.* 2015).

High competition during the tropical dry season, when critical resources are limited, may result in species exhibiting character displacement (e.g. Grant and Grant 2006, De Léon *et al.* 2014). Grant and Grant (2006) define it as an "evolutionary divergence in resource-exploiting traits such as jaws and beaks that is caused by interspecific competition." It leads to an accentuation of differences in certain traits between similar coexisting species. At sites where these species do not overlap in their ranges, differences in such traits may be minimal. *Geospiza* finches from the Galápagos Islands were the first birds in which the process of character displacement was described (Grant and Grant 2006). On the small Daphne Major Island, in the absence of a competitor, *G. fortis*' beak size was determined by a trade-off between rewards from feeding on small seeds (which are only abundant in the wet season) and large seeds (which are hard to crack but offer great rewards in the dry season; Grant and Grant 1993). A larger, more dominant competitor with similar ecological requirements can modify such a trade-off once it established its own breeding population. If it can access rewards from critical resources in the dry season more easily than the other species, and if it depletes them to such extent that it is no longer beneficial for the smaller bird to invest energy into trying to exploit them, a selective shift in morphology is predicted to occur (Grant and Grant 2006). Grant and Grant (2006) observed such a selective shift in bill-size in *G. fortis*, once the larger *G. magnirostris* inhabited Daphne Major, which gave start to an exploitative competition between the two species, resulting in a great decline in *G. fortis*' population until it adapted and thus found a way to avoid complete exclusion. The differences in foraging between seasons point at temporal segregation of resources.

Adding another dimension to the temporal aspect of niche partitioning is beneficial, yet rarely applied (De Léon *et al.* 2014). Niche partitioning occurs in time and space (e.g. Riegert *et al.* 2011), and while temporal niche differentiation describes a diversion in diet in periods of resource scarcity, spatial niche differentiation does the same in areas of resource scarcity (Miyazaki *et al.* 2006). Integrating both perspectives allows us to investigate which of them is a more deciding factor. Barrett *et al.* (2005) argue that spatial, temporal and spatiotemporal divergence in resources may result in the adaptive radiation of 'imperfect generalists'. Such species will exploit a variety of resources as long as they are abundant, and switch to private resources when competition is high—the dry season in the case of *Geospiza* finches. Particular resources are private for birds that are best specialized for exploiting them. De Léon *et al.* (2014)

merged the two dimensions of niche partitioning for the first time in *Geospiza* finches that live on a large island, measuring niche overlap not only between dry and wet seasons, but within the seasons, which are not always wet or dry in the same intensity. If the prediction mentioned in the previous paragraph is true, major differences in diet between related species should only be observed in times when resources are scarce (Robinson and Wilson 1998).

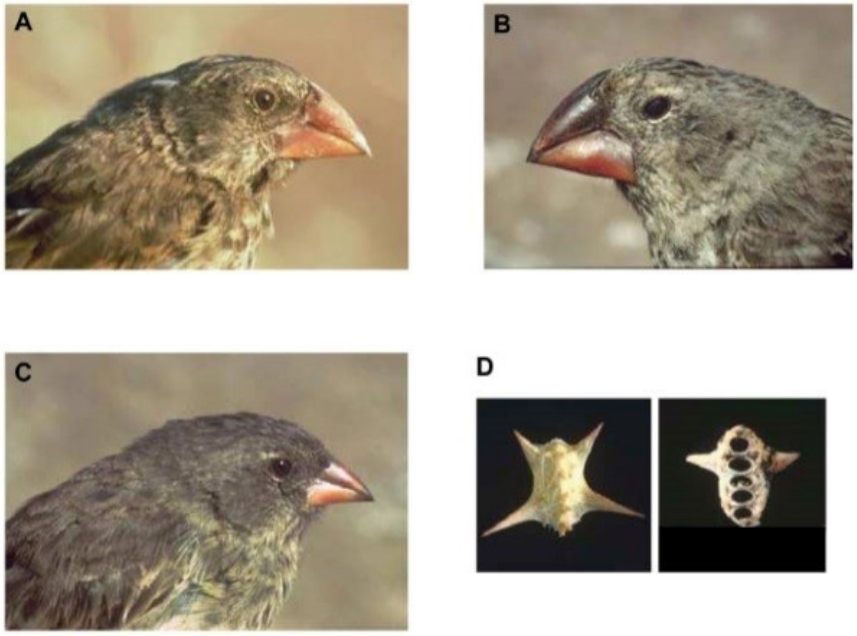

Fig. 1: Large-beaked *G. fortis* (A) and *G. magnirostris* (B) can exploit the hard-shelled *Tribulus cistoides* mericarps (D), while small-beaked *G. fortis* (C) cannot (Grant & Grant 2006).

De Léon *et al.* (2014) found that the *Geospiza* finches are imperfect generalists, exploiting a wide array of resources throughout the wet season, but restricting their diet to private resources in times of high competition. As I mentioned, not all wet seasons are equally wet, and niche overlaps grow with rising precipitation and weakening competition, especially in species that are the most similar in beak morphology. Some dry seasons may be extreme, and in such case, access to private resources is crucial for a population's survival (De Léon *et al.* 2014). The sympatric coexistence of such birds in a metacommunity dynamic is aided by frequency-dependent processes, where one taxon cannot eliminate another taxon that has private resources. This is because of spatiotemporal variation in diet and diet overlap, which does not allow any single of these species to become the superior competitor on any island (De Léon et al. 2014). In general, it has been found that island species are specialists, they exhibit an upper

limit of inter-specific competition tolerance, and in times of reduced competition, they expand into nontypical habitats (Terborgh and Faarborg 1980).

Character displacement does not have to be as prominent as it is in the previous example - such extremes are typical for islands (Norman *et al.* 2006). For instance, two syntopic species of warblers in mainland Brazil, *Basileuterus leucoblepharus* and *B. culicivorus*, maintain their coexistence by foraging in different strata and by using different foraging techniques, and do not exhibit significant differences in morphology (de Mendonça-Lima *et al.* 2004). Syntopy is a kind of sympatry in which two or more species forage in the same habitat at the same time. The dry season causes food to become scarce (De Léon *et al.* 2014), and/or self-maintenance to come with higher energetic costs (de Mendonça-Lima *et al.* 2004). Foraging heights differ for each of the two species between the seasons, significantly for *B. leucoblepharus* and less for *B. culicivorus*. *B. culicivorus* may find abundant prey more easily in summer and thus may not need to fly too high to find it, or it is pushed back by migrant birds who forage in the same strata. A greater, more significant change in the foraging range may be observed in *B. leucoblepharus*, who seems to choose to eat more visible prey in the summer, making its foraging range wider when resources are abundant.

A similar kind of resource subdivision has been confirmed in two scops owls from the Okinawa Island in Japan: *Otus elegans* and *O. semitorques* (Toyama and Saitoh 2011). They also subdivide resources by foraging in different strata. Few examples of congeneric syntopic owls have been reported thus far, and even those show significant variations in body size which allows the birds to coexist. Moreover, most syntopic owls belong to different genera, and maintain their coexistence by having different hunting techniques or choice of prey (Mikkola 1983 in Toyama and Saitoh 2011, Jaksić and Carothers 1985), which is consistent with the assembly rules (Diamond 1975). However, these two syntopic owls are congeneric, of similar size, overlap in prey choice, and even nest close to each other (>15 m, Toyama and Saitoh 2011). The plasticity of at least one party, in this case the rather opportunistic *O. semitorques*, seems to weaken the competitive pressures that are expected to exist between similar species. This species changes its diet according to availability, whereas *O. elegans*, consistently feeds on orthopterans in this sympatry, and therefore behaves as a specialist. *O. elegans*' diet outside this sympatry (on sites without *O. semitorques*) varies more, with

orthopterans only making up 25 % of its diet. Though this was not implied by the authors in their study, I think this population of *O. elegans*, being able to narrow its foraging niche in this sympatry, plays a great part in minimizing competition with this behaviour. However, no literature is available about *O. semitorques*'s feeding behaviour from sites without *O. elegans* (Toyama and Saitoh 2011), and the authors do not report aggressive encounters between the species, so this study itself is not enough to make further assumptions.

Furthermore, Diamond's (1975) fifth assembly rule predicts that certain species never co-occur (i.e. 'forbidden species combinations'), because species that have the same ecological requirements exclude each other from the same environment. This may result in a combination of checkerboard units in the range of a mixed-species flocks, where certain combinations of birds never coexist. In the Neotropics, this has been proved in mixed-species flocks of warblers (Parulidae) where *Setophaga cerulea* vs *S. castanea*, and *Chlorospingus flavigularis* vs *C. ophthalmicus* never co-occur (Colorado and Rodewald 2015). Further non-random co-occurrence patterns of mixed-species flocks have now been confirmed in more than twenty flocks in the Amazon Basin (Graves and Gotelli 1993), and the Andes (Colorado and Rodewald 2015). On the contrary, Gotelli and McCabe (2002) argue that checkerboard units may be the result of certain species' affinity for non-overlapping habitats, and not necessarily the result of competition.

Mixed-Species Flocks

Tropical birds are often specialized for using private resources. This allows tightly packed mixed-species communities to coexist, making specialization important for increasing species richness (Mohd-Azlan *et al.* 2014). Mixed-species flocks are typical in most tropical forests, but little is known about the structure and organization of these prevalent social systems in the tropics (Goodale and Kotagama 2005).

Wading birds typically aggregate in mixed-species flocks (e.g. Frederick and Bilstein 1992, Ishtiaq *et al.* 2010), and niche partitioning in such birds is relatively easy to study since such flocks are usually confined to foraging at a concrete site over a significant period. Wetlands offer a great variety of microhabitats that can be exploited, and they can also be exploited in different times of the day, allowing accordingly specialized species to avoid interference competition.

An unusually diverse community of ibises can be found in the central wetland plains of Venezuela (Frederick and Bildstein 1992): *Eudocimus ruber*, *Eudocimus albus*, *Plegadis falcinellus, Mesembrinibis cayennensis*, *Phimosus infuscatus*, *Cercibis oxycera*, and *Theristicus caudatus*. Frederick and Bildstein (1992) identify two species-assemblages within them, and this is how they partition resources during the critical, dry season:

The first assemblage consists of the first three abovementioned species, and they are all aquatic foragers, catching prey in waters above 3 cm. Not unexpectedly, most aggressive encounters within this species-assemblage happen between the two *Eudocimus* ibises (congeneric species). Their niches overlap the most: both take large prey, and they forage close to each other most of the time. Because of the striking similarity in behaviour and competitive abilities, and because they often interbreed, several authors argue that they may be races of the same species (Ramo and Busto 1987, Frederick and Bildstein 1992). *P. falcinellus* possibly became abundant in the wetlands of Venezuela in the last century, its position in the assemblage during the study might thus have been the result of that relatively recent arrival. All three species are large and more prone to exhibit aggressive behaviour than others. Because of their long legs, they may forage in deeper waters, and possibly because of body-size-dependent dominance taking place, they force the second assemblage to the edge of the water (Frederick and Bildstein 1992).

The next three abovementioned ibises prefer moist soil and edges of standing water when foraging, only choosing to forage in water when other species are absent. The two assemblages minimize possible competition between each other by choosing a different foraging habitat. Lastly, *T. caudatus* is the only species that is found foraging on dry land, and is rarely found in water. It therefore completely avoids competition for food with the other ibises (Frederick and Bildstein 1992).

Within-assemblage niche partitioning has also been observed by the authors. Behavioural avoidance and different microhabitat use seem to be the most significant mechanisms by which the members of the second assemblage maintain their coexistence. *Mesembrinibis cayennensis* spends most of the time foraging in shallow water, within approximately two meters of the shore, while *Cercibis oxycera* prefers to forage on moist soil and at the water's edge, in areas with little-to-no vegetation. *Phimosus*

infuscatus also forages on moist soil, but in areas with denser vegetation than *C. oxycera* (Frederick and Bildstein 1992).

Seasonal changes make foraging niches shift (Frederick and Bildstein 1992). The shift seems to be the most significant for *Eudocimus ruber*, which forages on moist soil in the wet season (Kushlan *et al.* 1985, van Wieringen and Brouwer 1990 in Frederick and Bildstein 1992), as well as for *Mesembrinibis cayennensis* and *Cercibis oxycera*, who also forage in the gallery-forest during the wet season. It is beneficial to emphasize that these shifts in foraging niches during the dry season allow for aggressive encounters to happen more often than they do in the wet season, when resources are plentiful. Finally, in comparison to other wading birds that ibises forage with, such as herons, egrets, or storks, they do not eat fish, which again minimizes competition between these birds (Frederick and Bildstein 1992).

In the Old World, Ishtiaq *et al.* (2010) found similar mechanisms of niche partitioning in storks from the Kuadalupe National Park in India. *Ephippiorhynchus asiaticus*, the tallest of them, has the longest bill, and is a solitary forager. *Anastomus oscitans* and *Mycteria leucocephala* are open-group foragers. The former is shorter and has a shorter bill than the latter (Ishtiaq *et al.* 2010). Body and bill dimensions may limit foraging abilities in certain depths. A long and wide bill provides a certain plasticity, the bird can feed on large and small prey equally. Other than water depth, vegetation density and risk of predation may also be factors that limit foraging success, and they do in the case of *M. leucocephala* (Ishtiaq *et al.* 2010). When a species' foraging strategy is to forage in groups and disturb a great amount of fish because of the presence of many individuals, flushing out hidden prey in the process (Master *et al.* 1993), it is preferred to do so in areas with minimal vegetation cover and away from dyke, because the extra amount of time spent on vigilance may be better utilized for hunting (Ishtiaq *et al.* 2010). Finally, *A. oscitans* forages in shallow waters or moist land, and does so in large groups, which may depress the effect of vigilance on foraging success – distance to dyke does not seem to lower the foraging success in this species as much as it does in *M. leucocephala* (Ishtiaq *et al.* 2010). Differences in their choice of prey add yet another dimension to the partitioning of their resources.

Bigger body size may determine dominance, which can then grant the bigger species access to a higher variety of resources. Differences in body size, foraging techniques and/or prey choice seem to be the main factors that allow closely related wading

birds to coexist, because they can exploit microhabitats they are specialized for. Toyama and Saitoh (2011) mention the body-size hypothesis in their study, too. According to this hypothesis, differences in body size determine whether species can coexist within a guild. Three typical and ecologically important guilds of tropical birds which have been included in niche partitioning studies are frugivores, nectarivores, and insectivores (Bregman *et al.* 2015), and that is the reason the rest of this chapter is dedicated to their foraging ecology, through which I aim to explain how these birds partition resources and maintain their coexistence.

Niche Partitioning within Tropical Guilds

A guild is defined as a group of species that exploit the same resources in a similar manner (Root 1967). These species may belong to different taxa and are not necessarily sympatric, but they need to have a significant overlap in niche requirements to be considered members of the same guild (Simberloff and Dayan 1991).

Frugivorous birds would be a vital study group for resource partitioning because zoochorous fruits have evolved to be easily found and consumed, which makes them easily spatio-temporally quantifiable (Howe and Smallwood 1982). They play an important role in seed dispersal and consequential forest regeneration (Walker 2006). But most studies involving tropical frugivorous birds focus on plant-bird interactions instead of their competition or coexistence with other frugivores (e.g. Walker 2006, Ragusa-Netto 2008, Ramos-Robles *et al.* 2016). While these studies are equally beneficial for the improvement of conservation efforts, they are irrelevant to my thesis, so I henceforth focus on the nectarivorous and the insectivorous guild.

The Nectarivorous Guild: Hummingbirds

Nectarivorous species are widely used models to study food-niche partitioning. Nectar-feeding birds are territorial and are known to defend resources for which they compete (e.g. Feinsinger 1976, Lara *et al.* 2009, Riegert *et al.* 2011, Weinstein and Graham 2016). Their food resources are easily observable since they are often displayed conspicuously (Gill and Wolf 1977), and many nectarivorous species affiliate to certain plants (Riegert *et al.* 2011). Nectar-feeding birds employ a range of foraging behaviours and partake in both interference and exploitation competition (Feinsinger *et al.* 1979). Birds are the second most important pollinators in the world after insects (Proctor *et*

al. 1996), and most of them feed on nectar, rather than pollen (Carstensen and Olesen 2009). A significant number of articles on niche partitioning in tropical covers the members of this guild, with hummingbirds (Trochilidae) in the Neotropics, sunbirds (Nectariinae) in the Afrotropics, and honeyeaters (Meliphagidae) in the Indo-Pacific biogeographical region being covered the most.

The only obligate nectarivorous birds in the New World are hummingbirds (Carstensen and Olesen 2009). They are the most specialized and best studied nectarivorous birds (Feinsinger *et al.* 1979), and for this reason I devote a reasonable part of this subsection to their foraging ecology. When comparing actual communities of hummingbirds to a regional species pool, closely related species co-occur much less often than one would expect (Weinstein and Graham 2016). Despite the expectation that aseasonal tropical forests provide year-round sources of nectar, some authors argue that the intensity of competition among hummingbirds is determined by resource abundance, and that resource subdivision is controlled by dominant birds via aggressive displacement (Feinsinger 1976, Weinstein and Graham 2016), so resource abundance must fluctuate. For instance, *Amazilia saucerottei*, a belligerent, dominant, territorial, and widespread species, has been shown to control the whole nectarivorous guild in a number of studied areas in Costa Rica (Feinsinger 1976). The bird forces subordinate individuals away aggressively, like many hummingbirds do (Weinstein and Graham 2016), and thus alters their foraging pattern. *A. saucerottei* restricts *Chlorostilbon canivetii*, a non-territorial principal species from the studied area, to flowers in lower-strata. This species is a trap-liner (i.e. it flies from flower to flower, since it can only exploit low-return feeders), and this skill can be utilized to force other non-territorial species to bypass dispersed low-return sources of food. In the absence of a dominant bird, however, species specialized for exploiting low-return feeders may switch to high-return feeders. This cannot be done the other way around (Feinsinger 1976).

Can two territorial birds coexist? Feinsinger (1976) argues that they can if they do not overlap extensively in their specialisms, or if one of the species regulates its own population density more than the other. However, a non-territorial trap-liner, or generalist, cannot coexist with another generalist, because the more efficient trap-liner makes the other switch to high-return sources in case of an encounter, or it can complete exclude it from the environment. Within-plant foraging differences (i.e. when one

species prefers higher or lower strata, or the inner or outer parts of the plant) also reduce competition (Feinsinger 1976). Again, adding another dimension to studying their niche partitioning is necessary. Temporal segregation depends on the time over which the plants renew food resources. Defending a plant is only profitable for the territorial bird if defending is more energy-efficient than ignoring it, so plants are only defended for a certain amount of time a day. This is useful for trap-liners or other birds who exploit poor-return resources, since they can exploit previously defended flowers (Feinsinger 1976). Weinstein and Graham (2016) argue that when resources are abundant, hummingbirds refrain from defending them, and instead visit flowers from a greater variety of plants. All in all, territorial species compete through interference, while non-territorial birds compete through exploitation (Feinsinger *et al.* 1979).

What I find intriguing in Feinsinger's (1976) study is that out of the 14 species of hummingbirds co-occurring in the successional forests of the Monteverde regions of Costa Rica, only two species have specialized bills, and the flowers in these successional forests have such shapes that even species with the shortest bill can exploit them. This means that their specialization plays little-to-no role here (Feinsinger 1976). These species can coexist without competitively excluding each other even though their niches overlap significantly (<10 % - 80 % over 14 months, inversely affected by resource availability; Feinsinger 1976). With differences in spatiotemporal foraging patterns, habitat preferences, and exploitation efficiencies, species can always find resources, or move to another community (Klopfer and MacArthur 1961). Finding out that competition drives feeding behaviour would be consistent with the ideal free distribution theory, which predicts that animals that exploit certain resources will aggregate in patches, in numbers that are proportional to the available amount of resources (Fretwell and Lucas 1969).

Keeping in mind the costs and benefits of defending private resources, similar findings to Feinsinger's (1976) study can be found in Lara *et al.*'s (2009) article on hummingbirds foraging on *Penstemon roseus* in Mexico. This plant is their limiting resource during the dry season, which means that many species rely on it as their most abundant source of food. This increases competition and thus forces hummingbirds to subdivide the resource. Small hummingbirds, such as *Selasphorus spp.* and *Calypte anna* visit lower flowers in a plant, which are also low in returns, and feed in earlier hours than the larger species, such as *Eugenes fulgens* and *Lampornis clemenciae*,

who prefer to feed on insects in the early morning to satisfy their energy requirements, and later switch to feeding on *P. roseus*. Small hummingbirds may choose to forage on *P. roseus* earlier to avoid aggression from the larger, territorial birds. Both Feinsinger (1976) and Lara *et al.* (2009) argue that temporal segregation may not be advantageous, because no energy is gained without feeding, so it should only occur when satisfying the energy requirements is not worth taking the risk of damage, which was the case in both studies, and in Weinstein and Graham's (2016) study as well. Moreover, Lara *et al.* (2009) argue that dominance hierarchy based on body size may determine which member of the assemblage gains access to nectar – small hummingbird species benefit from spatiotemporal niche segregation by avoiding conflict with bigger species. Nevertheless, Weinstein and Graham (2016) argue that a hummingbird's energetic budget greatly shapes behaviour. With more mass come higher energetic requirements, and this may explain why large hummingbirds exhibit great changes in selectivity with a growing resource abundance and smaller birds do not.

As for specialized species of hummingbirds, when resources are limited, they prefer to feed on flowers of such shape that corresponds with the length and shape of their bill (e.g. Wolf *et al.* 1976, Geerts and Pauw 2009, Maglianesi *et al.* 2015, Weinstein and Graham 2016). Like *Geospiza* finches who eat food that corresponds with the size and shape of their beak (De Léon *et al.* 2014), specialized hummingbirds feed on nectar from flowers shaped in a way that corresponds with their bill (Maglianesi *et al.* 2015). E.g. a long-curved bill species, *Phaethornis guy*, prefers long-curved flower types, the medium-size billed *Lampornis* calolaemus, though flexible in its preferences, usually inclines to feeding on medium-sized, plants and does not show preferences for flowers with a specific curvature, and *Eupherusa nigriventris* prefers short and straight flowers, since it has a short bill. Long-billed species are in an advantage, because they can exploit long and short flowers equally (Feinsinger 1976, Maglianesi *et al.* 2015). Still, they prefer long flowers. The reasons why long-billed hummingbirds still prefer feeding from flowers that match their beak is either that they hold higher rewards (Geerts and Pauw 2009), or because other birds cannot deplete nectar in such flowers, so there is always some left (Maglianesi *et al.* 2015). These findings show that morphological constraints may form the realized niche of hummingbirds, and are consistent with the optimal foraging theory which predicts that individuals will feed on the most profitable resources as long as they are sufficiently abundant (Sandlin 2000).

Moreover, Sandlin's (2000) study on similar species of hummingbirds, the dominant *Lampornis* clemenciae, and the subordinate *Archilocus alexandri* and *Eugenes fulgens*, focused on the idea that the birds' information state (i.e. the ability to predict the quality of the environment it forages in) may determine how they subdivide resources. An individual with incomplete information can only learn about the quality of environment by sampling from it, while an individual with complete information may be able to predict quality using cues, such as flower colour in this study. *A. alexandri* and other small hummingbirds switch to more generalist foraging methods when competition is high (Feinsinger and Colwell 1978, Sandlin 2000), as opposed to the dominant *L. clemenciae* who control distribution of resources and/or the amount of time available to feed on rich resources by belligerent behaviour. Finally, *E. flugens* is given special attention in Sandlin's (2000) article, because the author, as others (e.g. Feinsinger and Colwell 1978), fails to fit the species into any category of hummingbirds. It is called an 'interstitial species', which means it changes its competitive strategies in interaction with different species, in different locations. In the highlands of central Mexico, it is territorial, but still subordinate to *L. clemenciae*, in higher latitude, that is in southeastern Arizona it is no longer territorial but behaves as a 'high-reward trapliner', a strategy no other competitor in the area may employ (Sandlin 2000).

The Nectarivorous Guild: Sunbirds and Honeyeaters

Unfortunately, sunbirds nor honeyeaters have thus far been studied as extensively as hummingbirds, especially when it comes to analysing their coexistence (Carstensen and Olesen 2009). Studies on Paleotropic sunbirds are mostly limited to South Africa and the Tanzania-Kenya region, and mostly discuss the birds' physiology or their relationships with plants (Riegert *et al.* 2011). Nevertheless, I aim to discuss what is known so far.

Sunbirds occupy the same ecological niche as hummingbirds, but are less morphologically specialized to nectar-feeding, and often feed on insects by utilizing various foraging methods (Riegert *et al.* 2011). When they feed on nectar, they face an energetic problem just like hummingbirds – they need to increase their foraging efficiency (i.e. net energy gain per unit per time), because visiting flowers that had already been exploited is inefficient. Because of this, aggressive exclusion from previously unvisited

flowers may be beneficial (Gill and Wolf 1977). Just as territorial hummingbirds, territorial sunbirds may forage in one area that offers sucrose-rich resources until they are depleted. This depletion may increase resource patchiness, but if some flowers remain unvisited and constantly renew nectar, variance can be maintained (Gill and Wolf 1977). *Nectarinia reichenowi*, for instance, exhibits aggressive behaviour in competitive encounters when flowers produce high amounts of nectar (Gill and Wolf 1975). Chasing is a common form of aggressive behaviour imposed by the dominant *Cinnyris bouvieri* on *C. reichenowi* (Riegert *et al.* 2011), and is utilized when nectar is abundant enough to be defended. Nonetheless, inter-specific competition between the species is overall far less common than intra-specific competition. This may be due to their different choice of food (i.e. different plant species). The limited literature available on niche segregation in sunbird communities comes to similar conclusions, and the mechanisms behind niche partitioning in this group are not that different from hummingbirds.

Because of their similarity, sunbirds and honeyeaters in Southeast Asia are expected to exclude each other on small islands (Ripley 1959), but several examples of sympatries including these species exist. On the northern Moluccan Island of Batjan in eastern Indonesia, for example, two similar-sized species of sunbirds with identical feeding habits, *Nectarinia jugularis* and *Nectarinia sericea,* exist. These birds differ in climatic niches - the former inhabits coastal areas, forests, and man-made areas from sea-level to altitudes up to 106 m, while the latter was found over this altitude and below 152-182 m (Ripley 1959). Since their ranges do not overlap, they do not compete for resources. Instead, competition for resources occurs between the two sunbirds and a honeyeater (*Myzomela obscura*). The honeyeater is dominant over *N. sericea* during the breeding season even in sunbird territories, exhibiting aggressive behaviour toward the subordinate, but the population of honeyeaters here is small, which may aid coexistence via density-dependent habitat selection (see Feinsinger 1976; Ripley 1959).

The contact zone of Oriental sunbirds and Australian honeyeaters is Wallacea, Indonesia. It is the boundary between the Australian and Oriental biogeographical regions, and this boundary is especially rich in nectarivorous birds, with at least 122 identified species (Carstensen and Olesen 2009). Wallace's Line is the western boundary of Wallacea, and just as the region, this boundary is named after an English naturalist, Alfred Russell Wallace, who first pointed out a great difference between bird species

on either side (Wallace 1869). Bird species distributions in the area are well covered in scientific literature, but little is known about Wallacea's avifauna besides that, especially not about their community ecology (Cartensen and Olesen 2009).

The Australo-Papuan honeyeaters, are a widespread group of birds that range from being fully nectarivorous to fully insectivorous (Miller *et al.* 2013), and have diversified within forests, savannahs, mountains, and foothills (Norman *et al.* 2006). These birds exhibit great morphological and ecological variety, even between populations of a single species (races; Keast 1968), and this diversity is commonly attributed to segregation by ecological barriers or speciation via isolation on ecological islands (i.e. oceanic islands and mountain tops; Norman *et al.* 2006). Unfortunately, literature about niche partitioning in Meliphagidae is limited or focused on populations outside the tropics (e.g. Keast 1968, Slater 1994, Pearce *et al.* 1995). Instead, Australian honeyeaters are seen as vital models for studying evolution in climate space, since the family likely originated in wet forests that used to be widespread in Australia in the Eocene, but they now occupy semiarid and arid regions of the continent (Miller *et al.* 2013).

Habitat heterogeneity is the greatest in lower altitudes (below 2000 m; Norman *et al.* 2006), and as mentioned above, this allows for a high degree of niche partitioning. *Meliphaga* honeyeaters minimize competition between each other by having different bill morphologies, diverging in microhabitat selection and vertical zonation patterns, and while the processes of their diversification are not known, ecological and geographical mechanisms are evident (Norman *et al.* 2006).

In Australian savannah woodlands near Darwin, lorikeets and honeyeaters compete for nectar between the dry and wet seasons, and similarly to hummingbirds and sunbirds, the spatial segregation of foraging niches in these birds is only significant during times of resource scarcity (Noske and Franklin 1999). Nectarivorous specialists organize this community, and opportunists exploit resources that are left untouched by specialists. Two species here track nectar, *Trichoglossus moluccanus* (a lorikeet) and *Philemon citreogularis* (a honeyeater), but differ in spatial scales of doing so. However, competition for food between nectarivores in the woodlands of Northern Australia may not be high because nectar is never exploited completely. As a result, opportunists can occupy the available niches that are not filled by nectarivores (Noske and Franklin 1999).

The Insectivorous Guild

Poorer in nectarivores but richer in insectivores, bird communities in north Australian mangroves partition resources by differences in diet and foraging behaviour (Noske 1996). Mangroves in north Australia have the greatest avifaunal diversity of any other mangrove forests in the world, and offer seasonal resources for nectarivorous and insectivorous birds likewise (Mohd-Azlan *et al.* 2014). Moreover, they make up most of the tropical monsoon land on the continent. Mangrove birds in general have longer beaks, which allows them to take a wider range of food items. Being opportunistic feeders, the birds that live in mangrove communities partition resources only by utilizing different foraging strategies and taking different prey or nectar during the wet season. There is little-to-no evidence of competitive exclusion or interference competition taking place in this community. Species here are loosely packed (Mohd-Azlan *et al.* 2014). This is a trend in mangrove communities world-wide, possibly due to the simplicity of the habitat (e.g. Noske & Franklin 1999, Luther & Greenberg 2011). Few tree species typically dominate mangroves in contrast to rain forests, where species are more tightly packed and niche partitioning occurs in several resource dimensions (Mohd-Azlan *et al.* 2014). The species that make up mangrove bird communities in northeast Australia originated from the savannah matrix species pool, and have become dependent on mangrove ecosystems as the continent got dryer, making mangroves the only alternatives to evergreen forests (Nyári & Joseph 2012, 2013). This is a possible explanation as to why ecological processes may play little-to-no role in structuring assemblages in this environment (Mohd-Azlan *et al.* 2014).

An extensive study on niche partitioning occurring in more dimensions in tropical insectivorous birds (in relation to the number of species considered) was conducted near the Bukit Kepala Gajah limestone area in West Malaysia by Mansor and Mohd Sah (2012). Even within these birds, they identified three foraging guilds: "high-sally insectivores" who sally in high strata, "high-foliage insectivores" who forage using glean-stretch-hang tactics, and "understory insectivores" who forage in low strata. These mixed-species guilds consisted of a warbler (*Phylloscopus borealis*), a monarch (*Hypothymis azurea*), a paradise-flycatcher (*Terpsiphone paradisi*), a flycatcher (*Muscicapa dauurica*), an Erpornis (*Erpornis zantholeuca*), a iora (*Aegithina viridissima*), three babblers (*Macronous gularis*, *Malacocincla abbotti*, *Stachyris erythroptera*), and a prinia (*Prinia rufescens*). All species differ in foraging height, substrates,

and/or foraging techniques when they foraged at the same time, except for *T. paradisi* and *M. dauurica*, who overlap most in their foraging niche, but choose different habitats in relation to foliage density, and capture prey of different size, which may correspond with the body size differences between the two species of birds (Mansor and Mohd Sah 2012). Note that these birds are the most closely related to each other of all the birds in this sympatry. The authors emphasise that preferred vegetation density is a factor just as important in determining the extent of niche overlap as is foraging height, substrate, and attack manoeuvres (Mansor and Mohd Sah 2012), which is also true in the abovementioned example of coexisting storks (Ishtiaq *et al.* 2010).

Finally, the New World, antbirds (Thamnophilidae) are an important family of insectivorous birds. These birds are bioindicators of environmental quality because they are sensitive to changes in the environment (Ribon *et al.* 2003). They are territorial and monogamous, defending permanent territories, with both males and females exhibiting territorial behaviour (Mathias and Duca 2016).

Territoriality is possibly a ubiquitous feature for Neotropical insectivores (Greenberg and Gradwohl 1986). Territory sizes, however, tend to vary in different regions, and no data exist to explain why this is so (Mathias and Duca 2016). Territories of these birds tend to have a high overlap, which can only happen in case of niche partitioning, but more studies are needed to find out exactly how they are partitioned (Mathias and Duca 2016).

A lot of available studies about niche partitioning in insectivorous birds focus on intra-specific competition, and I therefore include these examples in a separate chapter, in which I discuss the often overlooked (Townsend Peterson and Holt 2003) niche partitioning within populations of a single species, that is between conspecific males and females, and between conspecific dominants and subordinates.

Chapter II

Niche-Based Assessments of Coexistence: Food-Niche Partitioning within Species

Many of the studies that address species coexistence focus on how species partition resources between each other, but in the end, the intensity of competition depends on the amount of resources available for any individual in space and time, and individual birds within a population may vary in the way they exploit these resources (Radford and du Plessis 2003). Pairs most often defend territories to prevent competition, but also individuals within these pairs can partition resources to be more effective in foraging and collecting of food for nestlings. It is therefore vital to examine whether similar mechanisms of partitioning can be found within populations of the same species. If partitioning of resources between members of the same species is predicted to occur, it should be a result of at least one of the three underlying factors at work: competition for food, differences in reproductive roles and sexual dimorphism (Freeman 2014). My aim in this short chapter is to discuss examples of intra-sexual and inter-sexual competition.

As opposed to interspecific competition, factors such as species diversity and relative aseasonality of tropical forests make intraspecific divergence in foraging behaviour less likely, according to Freeman (2014), and he further argues that this may be the reason most studies about sexual niche differentiation in tropics come from species-poor islands. I discuss examples from a variety of environments, but note that the observations are only relevant for particular populations that have been studied, and we should be cautious in making any generalized conclusions.

Intra-Specific Niche Partitioning: Sex and Dominance

Could competition for food between sexes result in a significant imbalance in sex ratios? The only population of *Alauda razae* inhabits the arid Raso islet in the Cape Verde Islands, often with fewer than 150 individuals (Ratcliffe *et al.* 1999, Donald *et al.* 2003, 2005, 2007), of which 65-75 % are male (Donald *et al.* 2005, 2007). These larks are sexually dimorphic, displaying differences in bill length and body size, with males being approximately 20% heavier than females (Donald *et al.* 2007), which may

promote territorial behaviour because of greater energetic requirements, making resource defence beneficial (Weinstein and Graham 2016). Males and females compete for plant bulbs which are one of the main sources of nutrients and water—there is no freshwater source on the islet. Both sexes are equally efficient diggers, but males utilize this behaviour more often than females, who instead pick food from the surface in the presence of males. Males, being larger and dominant, tend to steal food from females, or aggressively exclude them from the competed foraging range. Dominant males also tend to exclude smaller, weaker males, from their foraging habitat, making digging more profitable for themselves than for smaller males or females (Donald *et al.* 2007). Consequently, females experience high food stress, which may be the reason females make up only 25-35 % of the population – this has been described in other birds (e.g. Whittingham *et al.* 2004). The higher predation risk of females reinforces this imbalance due to less time devoted to vigilance (Donald *et al.* 2003). Rather than reduce competition, this kind of dominant male behaviour seems to competitively exclude females from a highly nutritious food source. Sexual dimorphism is present in the species, but although sexual differences in foraging may be linked to dimorphism in body size in general, the relationship does not have to be causal. Donald *et al.* (2003) did not find a correlation between foraging behaviour and differences in beak shape or size, so sexual dimorphism is not the reason for sexual differences in foraging. Unfortunately, the authors do not offer a theoretical account to this behaviour, nor do they offer any idea which would describe how females compensate for the abovementioned competitive exclusion (Donald *et al.* 2007). I find this situation very similar to the one involving *Geospiza* finches (Grant and Grant 2006), so it will be interesting to observe how it evolves.

Another complex example of food resource subdivision between members of the same species comes from Radford and du Plessis (2003), who report sexual differences in the food niche of the sexually dimorphic green woodhoopoes (*Phoeniculus purpureus*), where dominant males probe holes in bark more often than females, who instead mostly pick food from the surface of trees. The authors of this study conclude that the extreme dimorphism in bill length (about 37% difference) of the green woodhoopoes may indeed be associated with differences in foraging, rather than a result of sexual selection (Radford and du Plessis 2003, Wright and Radford 2010).

Phoeniculus purpureus are cooperatively breeding birds from sub-Saharan forests. Most studies regarding cooperative breeders focus on the foraging ecology of their populations as a whole, and mostly aim to explain these systems by types and distributions of food resources – they seldom offer observations of individual foraging behaviour (Wright and Radford 2010). *P. purpureus* forage in groups led by a dominant pair, and often on the same tree, which allows for intra- and intersexual competition to take place. Sex- and dominance-specific differences in foraging strategies within such groups may be shaped by state-dependent behaviours (e.g. Cuthill *et al.* 1997 in Wright and Radford 2010, Lange and Leimar 2004). It is expected that sexual dimorphism prevents dominants from inter-sexual displays of aggressive behaviour (Radford and du Plessis 2003), which consequently allows both sexes to forage side by side. Because of their morphological differences, they may utilize different foraging methods and thus sub-divide resources, minimizing competition as a result.

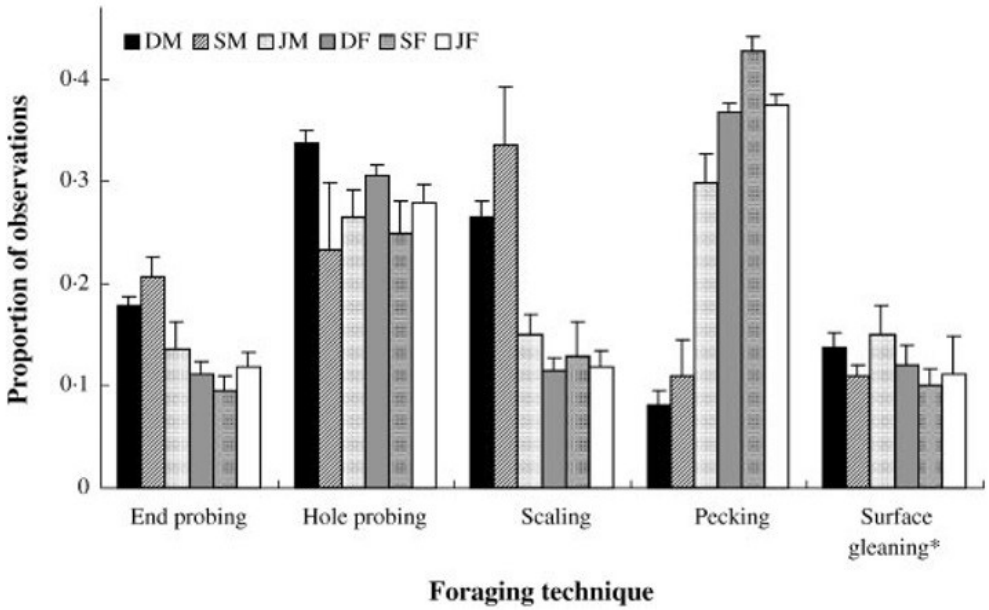

Fig. 2: Differences in foraging technique preferences of dominant males (DM), subordinate males (SM), juvenile males (JM), dominant females (DF), subordinate females (SF), and juvenile females (JF; Radford and du Plessis 2003).

Differences in foraging behaviour resulting from morphological differences provide evidence for the specialization hypothesis (Radford and du Plessis 2003), but the fact that both sexes of *Phoeniculus purpureus* can use the same foraging techniques with similar levels of success goes against it (Wright and Radford 2010). Sexual niche

segregation does not cause significant differences in foraging rewards, here understood as success rates and prey sizes obtained, which means that sexes do not directly benefit from their specializations (Radford and du Plessis 2003).

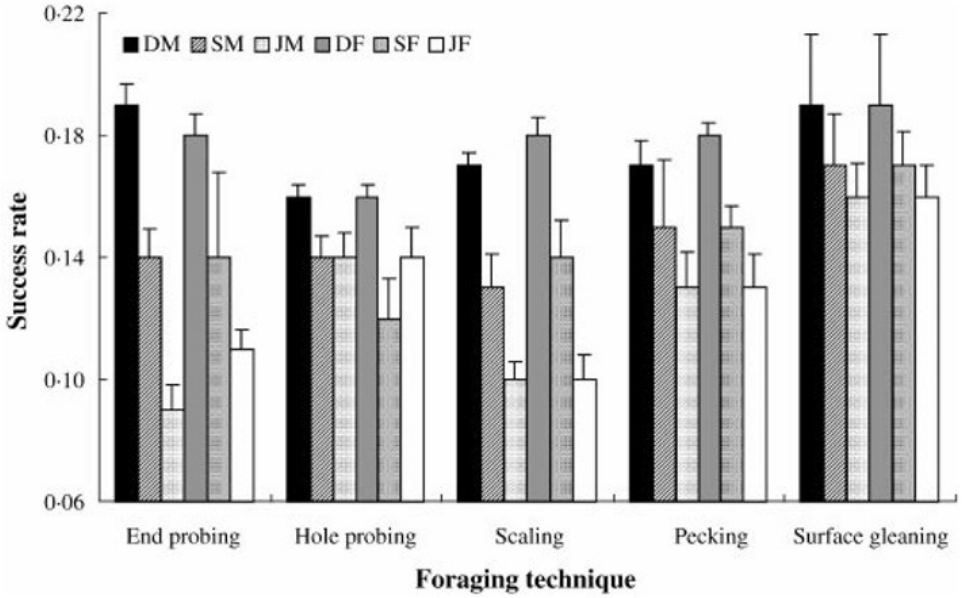

Fig. 3: Similarity of foraging success rates between males and females of the same dominance class utilizing the same foraging technique (Radford and du Plessis 2003).

Wright and Radford (2010) suggest that sex differences in foraging behaviour are based on variance-sensitivity in foraging returns (success rates and prey sizes obtained), rather than on differences in mean prey capture using a certain foraging method. Individuals risk that variable returns end up getting much poorer returns than the average. This kind of risking may become adaptive in cooperative species, and some members can consequently become variance-prone or variance-averse (Wright and Radford 2010). The reason for this is that daily energy requirements may differ between males and females, and between dominants and subordinates, too. Females are more variance-averse and males more variance-prone, meaning that females prefer to utilize foraging methods that provide for a consistency in foraging returns, while males do the opposite. The short bills of females evolved to limit variance in foraging returns when using risky (i.e. less preferred) techniques, and the long bill of the males promotes such variance. This is consistent with the risk-sensitivity theory, also called variance-sensitivity theory (Wright and Radford 2010). Moreover, the authors suggest that, because of their inexperience and competitive inability, subordinates are less successful in foraging than dominants.

Sexual niche partitioning may also occur in species with no, or limited, sexual dimorphism (Recher and Holmes 2000, Freeman 2014). Freeman's (2014) study of two whistlers, *Pachycephala schlegelii* and *Pachycephala soror*, from the montane forests of New Guinea provides one of the few evidences of such partitioning in tropical birds from continental tropical environments. The two species of whistlers feed on insects, but they are not cooperative breeders and show limited sexual dimorphism, with males having longer wings than females, thus being slightly bigger, and possibly dominant (Freeman 2014). Both species are territorial and monogamous with biparental care and both forage in pairs or join mixed-species flocks. Males of each species observed in Freeman's (2014) study foraged in higher strata than females, and females were caught in ground-level nets more often than males (twice as often in *P. schlegelii*, and four times in *P. soror*).

Freeman (2014) suggests that year-round competition for food among sexes is the driver of the observed spatial niche partitioning, and not sexual dimorphism (because it is limited in whistlers) or differences in reproductive roles. The reproductive-role hypothesis predicts that differences in foraging behaviour may arise from differences in reproductive roles. Generally, females may prefer to forage near nests in the breeding season, while males may prefer to forage in areas where vigilant territorial behaviour is allowed (e.g. Morse 1968, Morimoto and Wasserman 1991). Not a lot is known the time of breeding of either species, nor about the nesting behaviour of regent whistlers. *Pachycephala soror* do build nests in the understory, which may support the hypothesis, but most birds caught by Freeman did not exhibit signs of breeding, such as brood patches in females or cloacal protuberances in males, which means most whistlers were not breeding at that time. This observation was enough for Freeman (2014) to conclude that the differences in foraging among sexes were not connected to breeding. To further examine the mechanistic basis of the niche partitioning, removal experiments would be necessary. The author claims that apart from his, there is only one other study that confirms sex differences in a continental tropical species of birds, albeit he mentions Radford and du Plessis's (2003) study on the *Phoeniculus purpureus*, too. Still, sex niche partitioning in the tropics seems to be a highly unexplored yet clearly fruitful topic.

Sex niche partitioning in the Neotropics has also been documented in hummingbirds. *Lara et al.* (2009) report sex differences in foraging methods of hummingbirds

feeding on the nectar of *Penstemon roseus*. Typically, according to Lara *et al.* (2009), *Penstemon roseus* plants that grow in territories defended by white-eared hummingbirds (*Hylocharis leucotis*) offer such foraging grounds for females, where they can feed with impunity, as long as they feed on the flowers that grow on the lower parts of the plant. When they move to upper flowers, they are instantly forced to leave by territorial males. Hummingbird communities have a dominance hierarchy, as described in the previous chapter, therefore this resource partitioning may minimize aggressive encounters (Lara *et al.* 2009).

Intra-Specific Niche Partitioning: An Explanation for Partial Migration?

Intra-specific competition for resources can be reduced by temporal changes in habitat choice as well (Jahn *et al.* 2010). Several tropical bird species partially migrate to more favourable areas within the tropics, and such migration can be obligatory or facultative. In case of facultative partial migration, factors such as asymmetry in body size or frequency-dependency (abundance of subordinates vs. dominants) determine which individuals will migrate. This is the case for the insectivorous and territorial *Tyrannus melancholicus* at the Caparú Biological Station in Belize. This population can only survive the dry season, when insects are rare, if certain members seasonallz leave the area and migrate to resource-rich habitats, i.e. only individuals of certain size and social status can coexist at that time (Jahn *et al.* 2010). Large and dominant adult males are more likely to migrate since they have already established their territories and they may reclaim them the following breeding/wet season (see Cristol *et al.* 1999). For hatch-year males, it is beneficial to remain in the same area because they can learn about new territories without being limited by dominants (Jahn *et al.* 2010). Adult females are less likely to migrate because, as other migrant species (see Harper 1985), they may risk late breeding-pair formation, while hatch-year females are more likely to migrate because they risk exclusion by more dominant females from the few remaining resources (Jahn *et al.* 2010). Moreover, males are larger than females, and because of the greater energetic requirements deriving from a greater body size, males are expected to be the sex that migrates – the remaining resources would not satisfy their energetic needs.

Partial migration may thus serve to minimize competition for resources between sexes and between dominants and subordinates of the same sex. These findings are

close to those of Boyle (2008), who studied a similar situation in a manakin, *Corapipo altera*. In addition, though, Jahn *et al.* (2010) argue that the existing hypotheses only offer partial explanations for this behaviour, and that the available literature regarding this behaviour in the Neotropics cannot be used to make generalized notions about other migratory systems. Also, a lot of their predictions arise from studies on migrants conducted in the temperate zone (e.g. Harper 1985, Cristol *et al.* 1999). More studies in the tropics, and in this case a study conducted in the overwintering location of *T. melancholicus* would be necessary to find out why migration is more beneficial to this population, rather than any other form of resource partitioning, perhaps less energy-demanding.

Even though species diversity and the aseasonality of tropical environments closer to the equator may be seen as a factor that does not promote sex niche partitioning (Freeman, 2014), various examples of such partitioning show that differences in feeding behaviour among sexes do exist, and are perhaps more common than thought, in both sexually dimorphic and monomorphic species. Furthermore, differences in foraging strategies within and among individuals also contribute to the niche breadth of a population (Feinsinger *et al.* 1979). Assessing differences between, and the requirements of individuals can better conservation efforts in the highly disturbed tropical ecosystems, but the extent of how these finding can be applied seems to be unclear.

Conclusion

Overall, inter- and intra-specific niche differentiation is aided by a variety of mechanisms that differ from one location to another. Dominant birds actively defend resources if such behaviour is energetically efficient, and subordinate species exploit those resources that are left untouched, and it has been shown that even a single species can control the structure of communities (e.g. Feinsinger 1976). Differences in foraging niches are most evident when resources become scarce, or in the presence of migrants (e.g. de Mendonça-Lima *et al.* 2004). The size of habitats which include a variety of niches is the most important factor that in allows tropical species to coexist, and this has been shown in studies of fragmented forests (e.g. Bregman *et al.* 2015).

The greatest challenge in defining the underlying mechanisms that drive species coexistence in the diverse tropical ecosystems lies in finding adequate literature to back-up observed findings. That is a problem that has met a great number of authors studying any form of niche partitioning covered in this thesis (e.g. de Mendonca-Lima *et al.* 2004, Jedlicka *et al.* 2005, Mansor and Mohd Sah 2012, Freeman 2014). More studies are needed to corroborate many findings, but it is clear that mechanisms of coexistence vary greatly in all groups that have been considered, and that niche partitioning must be assessed in several dimensions to allow us to reach more accurate conclusions (De Léon *et al.* 2014).

One evident feature of my thesis is its gradual shift from discussing examples of niche partitioning between species or ecological groups of birds, to discussing niche partitioning in particular populations and between individuals within them. Rodríguez *et al.* (2015) analysed the recent form of niche assessment, and according to the authors, the classical niche concept does not fit into ecosystems with high species diversity, because its current form relies on the concept of population. On this level, the outcome of competition between populations of two species relies on both parties' behavioural plasticity, and not only of the populations themselves, but on the plasticity of individuals within them, too, as is evident in Chapter II. The number of very similar individuals belonging to a particular species will continuously decline with a further increase in ecological patchiness, while species diversity is expected to continuously grow (Rodríguez *et al.* 2015). Moreover, Townsend Peterson and Holt (2003) found

that different populations of the same tropical species in various latitudinal zones occupy different niches, based on geographical variations of occupied environments. On top of that, conspecifics may be seen as ecologically identical only if niche variation between individuals is weak or has little-to-no effect on ecological processes (Bolnick *et al.* 2003). In theory, differences in niches facilitate frequency-dependent interactions, and those promote population stability and regulate the collapse of biodiversity in fragmented ecosystems (Bregman *et al.* 2015). It has been suggested that niche partitioning on the level of an individual is important in shaping these interactions more than generally thought (Bolnik *et al.* 2003), making it an interesting topic for further research.

Most of the abovementioned authors hope that the results of their studies will be useful in improving conservation efforts. Assemblies of bird communities in the tropical forests are highly affected by fragmentation, specifically by fragment size (Bregman *et al.* 2015). Decreasing patch size intensifies competition because it reduces the availability of resources, and because each species has its minimum area requirements. Consequently, birds tend to be more generalist in fragmented areas than their conspecifics in less fragmented forests, according to Bregman *et al.* (2015). The lack of resources and space may result in ecologically similar birds (i.e. those with high niche overlap) competitively excluding each other, possibly leading to a local extinction. Moreover, fragmentation causes environmental changes, which may in turn increase mortality in many ways. Bregman *et al.* (2015) found that "extinctions driven by the reduction in size, habitat quality, and connectedness of rain forest fragments are nonrandom, and mediated by niche-based interactions among related species."

Habitat loss *per se* is not the only driver of tropical avian extinctions, but active biotic processes too (Feeley and Terborgh 2008). Because of this, studies focusing on niche partitioning and competition in bird communities should further serve to improve conservation efforts, providing vital information about the ecological requirements of coexisting birds in a variety of habitats.

Bibliography:

Abrams, P. A. (1989) The importance of intraspecific frequency-dependent selection in modeling competitive coevolution. *Evolutionary Ecology* 3, 215-220. DOI: 10.1007/BF02270722

Arellano, G., Umaña, M. N., Macia, M. J., Loza, M. I., Fuentes, A., Cala, V., Jørgensen, P. M. (2017) The role of niche overlap, environmental heterogeneity, landscape roughness and productivity in shaping species abundance distributions along the Amazon–Andes gradient. *Global Ecology and Biogeography* 26, 191-202. DOI: 10.1111/geb.12531

Barrett, R.D., MacLean, R.C. & Bell, G. (2005). Experimental evolution of *Pseudomonas fluorescens* in simple and complex environments. *The American Naturalist* 166, 470–480. DOI: 10.1086/444440

Birch, L. C. (1957) The meanings of competition. *The American Naturalist* 91, 5-18. DOI: 10.1086/281957

Boyle, W.A. (2008) Partial migration in birds: tests of three hypotheses in a tropical lekking frugivore. *Journal of Animal Ecology* 77, 1122–1128. DOI: 10.1111/j.1365-2656.2008.01451.x

Bregman, T. P., Lees, A. C., Seddon, N., MacGregor, H. E. A., Darski, B., Aleixo, A., Bonsall, M. B. & Tobias, J. A. (2015) Species interactions regulate the collapse of biodiversity and ecosystem function in tropical forest fragments. *Ecology* 96, 2692-2704. DOI: 10.1890/14-1731.1.sm

Brown, W. L. & Wilson, E. O. (1956) Character displacement. *Systematic Zoology* 5, 49-64. DOI: 10.2307/2411924

Bulmer, M. G. (1974) Density-dependent selection and character displacement. *The American Naturalist*, 108, 45-58. DOI: 10.1086/282884

Carstensen, D. W. & Olesen, J. M. (2009) Wallacea and its nectarivorous birds: nestedness and modules. *Journal of Biogeography* 36, 1540-1550. DOI: 10.1111/j.1365-2699.2009.02098.x

Cody, M. L. (1985) Habitat selection in birds. Academic Press, New York

Colorado, G. J. & Rodewald, A. D. (2015) Assembly patterns of mixed-species avian flocks in the Andes. *Journal of Animal Ecology* 84, 386–395 DOI: 10.1111/1365-2656.12300

Colwell, R. K. & Futuyma, D. J. (1971) Measurement of niche breadth and overlap. *Ecology* 52, 567-576. DOI: 10.2307/1934144

Cristol, D. A., Baker, M. B. & Carbone, C. (1999) Differential migration revisited: latitudinal segregation by age and sex class. *Current Ornithology* 15, 33–88. DOI: 10.1007/978-1-4757-4901-4_2

*Cuthill, I. C. & Houston, A. I. (1997) Managing time and energy. In: Behavioural Ecology: An Evolutionary Approach, 4th edn (Krebs, J. R. & Davies, N. B., eds). Blackwell, Oxford, pp. 97—120

Darwin, C. R. (1859) On the origin of species by means of natural selection. John Murray, London, UK.

Diamond, J. M. (1975) Assembly of species communities. Pages 342-444 in M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.

Donald, P. F., de Ponte, M., Pitta Groz, M. J. & Taylor, R. (2003) Status, ecology, behaviour and conservation of Raso Lark *Alauda razae*. *Bird Conservation International* 13, 13–28. DOI: 10.1017/S0959270903003022

Donald, P. F., de Ponte, M., Pitta Groz, M. J., Taylor, R., Wells, C. E., Marlow, T. & Hille, S. (2005) Status of Raso Lark *Alauda razae* in 2003, with further notes on sex ratio, behaviour and conservation. *Bird Conservation International* 15, 165–172. DOI: 10.1017/S0959270905000134

Donald, P. F., Hille, S., de L. Brooke, M., Taylor, R., Wells, C. E., Bolton, M. & Marlow, T. (2007) Sexual dimorphism, niche partitioning and social dominance in the feeding ecology of the critically endangered Raso Lark *Alauda razae*. *Ibis* 149, 848-852. DOI: 10.1111/j.1474-919X.2007.00701.x

Feeley and Terborgh (2008) Direct versus indirect effects of habitat reduction on the loss of avian species from tropical forest fragments. *Animal Conservation* 11, 353-360. DOI: 10.1111/j.1469-1795.2008.00182.x

Feinsinger, P. (1976) Organization of a tropical guild of nectarivorous birds. *Ecological Monographs* 46, 257–291. DOI: 10.2307/1942255

Feinsinger, P., Colwell, R. K. (1978) Community organization among neotropical nectar-feeding birds. *American Zoologist* 18, 779-795. DOI: 10.1093/icb/18.4.779

Feinsinger, P., Colwell, R. K., Terborgh J. & Budd Chaplin, S. (1979) Elevation and the morphology, flight energetics, and foraging ecology of tropical hummingbirds. *The American Naturalist* 113(4), 481-497. DOI: 10.1086/283408

Freeman, B. (2014) Sexual niche partitioning in two species of New Guinean *Pachycephala* whistler. *Journal of Field Ornithology* 85, 23-30. DOI: 10.1111/jofo.12046

Frederick, P. C. & Bildstein, K. L. (1992) Foraging ecology of seven species of neotropical ibises (Threskiornithidae) during the dry season in the llanos of Venezuela. *The Wilson Bulletin* 104, 1-21. DOI: unavailable

Gaston, K. J., Blackburn, T. M. (1996) The tropics as a museum of biological diversity: An analysis of the New World avifauna. Proceedings: *Biological Sciences* 263, 64-68. DOI: 10.1098/rspb.1996.0011

Gause, G.F., (1934a) Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. *Science* 79, 16–17. DOI: 10.1126/science.79.2036.16-a

Geerts, S. & Pauw, A. (2009) Hyper–specialization for long–billed bird pollination in a guild of South African plants: the Malachite Sunbird pollination syndrome. *South African Journal of Botany* 75, 699–706. DOI: 10.1016/j.sajb.2009.08.001

Gill, F. B. & Wolf, L. L. (1975) Economics of feeding territoriality in the Golden-Winged Sunbird. *Ecology* 56, 333-345. DOI: 10.2307/1934964

Gill, F. B. & Wolf, L. L. (1977) Nonrandom foraging by sunbirds in a patchy environment. *Ecology* 58, 1284-1296. DOI: 10.2307/1935081

Goodale, E. & Kotagama, S. W. (2005) Testing the roles of species in mixed-species bird flocks of a Sri Lankan rain forest. *Journal of Tropical Ecology* 21, 669-676. DOI: 10.1017/S0266467405002609

Gotelli, N. J. & McCabe, D. J. (2002) Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. *Ecology* 83, 2091-2096. DOI: 10.2307/3072040

Grant, B. R. & Grant, P. R. (1993) Evolution of Darwin's finches caused by a rare climatic event. Proceedings: *Biological Sciences* 251, 111-117. DOI: 10.1098/rspb.1993.0016

Grant, P. R. & Grant, B. R. (2006) Evolution of character displacement in Darwin's finches. *Science* 313, 224-226, DOI: 10.1126/science.1128374

Hau, M., Perfito, N., and Moore, I.T. (2008). Timing of breeding in tropical birds: Mechanisms and evolutionary implications. *Ornitologia Neotropical* 19, 39–59. DOI: unavailable

Hardin, G. (1960) Competitive exclusion principle. *Science* 131, 1292-1297. DOI: 10.1126/science.131.3409.1292

Harper, D.G.C. (1985) Pairing strategies and mate choice in female robins *Erithacus rubecula*. *Animal Behaviour* 33, 862–875. DOI: 10.1016/S0003-3472(85)80020-8

Howe, H. F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13, 201-228. DOI: 10.1146/annurev.es.13.110182.001221

Ishtiaq, F., Javed, S., Coulter, M. C., Rahmani, A. R. (2010) Resource partitioning in three sympatric species of storks in Keoladeo National Park, India. *Waterbirds* 33, 41-49. DOI: 10.1675/063.033.0105

Jahn, A. E., Levey, D. J., Hostetler, J. A. & Marnani, A. M. (2010) Determinants of partial bird migration in the Amazon Basin. *Journal of Animal Ecology* 79, 983-992. DOI: 10.1111/j.1365-2656.2010.01713.x

Jaksić, F.M. & Carothers, J.H. (1985) Ecological, morphological, and bioenergetic correlates of hunting mode in hawks and owls. *Ornis Scandinavica* 16, 165– 172. DOI: 10.2307/3676627

Janzen, D. H. (1967) Why mountain passes are higher in the tropics. *The American Naturalist* 101, 233-249. DOI: 10.1086/282487

Keast, A. (1968) competitive interactions and the evolution of ecological niches as illustrated by the Australian honeyeater genus *Melithreptus* (Meliphagidae). *Evolution* 22, 762-782. DOI: 10.2307/2406902

Klopfer, P. H., and R. H. MacArthur (1960) Niche size and faunal diversity. *The American Naturalist* 96, 293-300. DOI: 10.1086/282130

Klopfer, P. H., and R. H. MacArthur (1961) On the causes of tropical species diversity: Niche overlap. *The American Naturalist* 95, 223-226. DOI: 10.1086/282179

Kushlan, J. A., Morales, G., Frohring, P. C. (1985) Foraging niche relations of wading birds in tropical wet savannas. *Ornithological Monographs* 36, 663-682. DOI: 10.2307/40168311

*Lack, D. (1971) Ecological isolation in birds. Blackwell Scientific, Oxford, UK.

Lange, H. & Leimar, O. (2004) Social stability and daily body mass gain in great tits. Behavioural *Ecology* 15, 549—554. DOI: 10.1093/beheco/arh044

Lara, C., Lumbreras, K. & Gonzáles, M. (2009). Niche partitioning among hummingbirds foraging on *Penstemon roseus* (Plantaginaceae) in Central Mexico. *Ornitologia Neotropical* 20, 73-83. DOI: unavailable

de Léon, L. F., Podos, J., Gardezi T., Herrel, A. & Hendry, A. P. (2014) Darwin's finches and their diet niches: the sympatric coexistence of imperfect generalists. *Journal of Evolutionary Biology* 27, 1093–1104, DOI: 10.1111/jeb.12383

Lutger, D. & Greenberg, R. (2011) The island syndrome in coastal wetland ecosystems: convergent evolution of large bills in mangrove passerines. *Auk* 128, 201–204. DOI: 10.1525/auk.2011.10262

MacArthur, R. H. (1958) Population Ecology of Some Warblers of Northeastern Coniferous Forests. *Ecology* 39(4), 599-619. DOI: 10.2307/1931600

Maglianesi, M. A., Böhring-Gaese, K. & Schleuning, M. (2015) Differnet foraging preferences of hummingbirds on artificial and natural flowers reveal mechanisms structuring plant-

pollinator interactions. *Journal of Animal Ecology* 84, 655-664. DOI: 10.1111/1365-2656.12319

Mansor M. S., Mohd Sah S. A. (2012) Foraging patterns reveal niche separation in tropical insectivorous birds. *Acta Ornithologica* 47, 27–36. DOI: 10.3161/000164512X653890

Martin, R. O., Cunningham, S. J. & Hockey, Ph. A. R. (2015) Elevated temperatures drive fine-scale patterns of habitat use in a savanna bird community. *Ostrich* (2015):xxx-xxx. DOI: 10.2989/00306525.2015.1029031

Master, T. L., Frankel, M. & Russell, M. (1993) Benefits of foraging in mixed-species wader aggregations in a southern New Jersey saltmarsh. *Colonial Waterbirds* 16, 149-157. DOI: 10.2307/1521433

Mathias, L. B. & Duca, Ch. (2016) Territoriality of six Thamnophilidae species in a cloud forest in southestern Brazil. *The Wilson Journal of Ornithology* 128, 752-759. DOI: 10.1676/15-184.1

de Mendonça-Lima, A., Hartz, S. M. & Kindel, A. (2004) Foraging behavior of the white-browed (*Basileuterus leucoblepharus*) and the golden-crowned (*B. culicivorus*) warblers in a semidecidual forest in Southern Brazil. *Ornitologia Neotropical* 15, 5-15. DOI: unavailable

*Mikkola, H. (1983) Owls of Europe. Buteo Books, Vermillion, SD U.S.A.

Miller, E. T., Zanne, A. E. & Ricklefs, R. E. (2013) Niche conservatism constrains Australian honeyeater assemblages in stressful environments. *Ecology Letters* 16, 1186-1194. DOI: 10.1111/ele.12156

Miyazaki, T., Tainaka, K., Togashi, T., Suzuki, T. & Yoshimura, J. (2006) Spatial coexistence of phytoplankton species in ecological timescale. *Population Ecology* 48, 107–112. DOI: 10.1007/s10144-006-0256-1

Mohd-Azlan, J., Noske, R. A. & Lawes, M.J. (2014) Resource partitioning by mangrove bird communities in north Australia. *Biotropica* 46, 331-340. DOI: 10.1111/btp.12108

Morimoto, D. C., & Wasserman, F. E. (1991) Intersexual and interspecific differences in the foraging behavior of Rufous-sided Towhees, Common Yellowthroats and Prairie Warblers in the Pine Barrens of southeastern Massachusetts. *Journal of Field Ornithology* 62, 436–449. DOI: unavailable

Morse, D. H. (1968) A quantitative study of foraging of male and female spruce-woods warblers. *Ecology* 49, 779–786. DOI: 10.2307/1935549

Nyári, Á. S. & Joseph, L. (2012) Evolution in Australasian mangrove forests: multilocus phylogenetic analysis of the Gerygone Warblers (Aves: Acanthizidae). *PLoS One* 7, e31840. DOI: 10.1371/annotation/2e9dfd8d-413c-47bd-84c2-d7df5db7859c

Nyári, Á. S. & Joseph, L. (2013) Comparative phylogeography of Australo-Papuan mangrove-restricted and mangrove-associated avifaunas. *Biological Journal of the Linnean Society* 109, 574-598. DOI: 10.1111/bij.12082

Noske, R. A (1996) Abundance, zonation and foraging ecology of birds in mangroves of Darwin Harbour, Northern Territory. *Wildlife Research* 23, 443-474. DOI: 10.1071/WR9960443

Noske, R. A. & Franklin, D. C. (1999) Birds and nectar in a monsoonal woodland: correlations at three spatio-temporal scales. *EMU* 99, 15-28. DOI: 10.1071/MU99003

Norman, J. A., Rheindt F. E., Rowe, D. L. & Christidis, L. (2006) Speciation dynamics in the Australo-Papuan *Meliphaga* honeyeaters. *Molecular Phylogenetics and Evolution* 42, 80-91. DOI: 10.1016/j.ympev.2006.05.032

Pearce, J., Menkhorst, P. & Burgman, M. A. (1995) Niche overlap and competition for habitat between the Helmeted Honeyeater and the Bell Miner. *Wildlife Research* 22, 633-46. DOI: 10.1071/WR9950633

Primack, R.B., and Corlett, R. (2005) Tropical rain forests: an ecological and biogeographical comparison. Wiley-Blackwell, Oxford, UK.

Radford, A. N., du Plessis, M. A. (2003) Bill dimorphism and foraging niche partitioning in the green woodhoopoe. *Journal of Animal Ecology* 72, 258-269. DOI: 10.1046/j.1365-2656.2003.00697.x

Ragusa-Netto, J. (2008) Toco Toucan feeding ecology and local abundance in a habitat mosaic in the Brazilian cerrado. *Ornitologia Neotropical* 19, 345-359. DOI: unavailable

Ramo, C. & Busto, B. (1987) Hybridization between the Scarlet Ibis (*Eudocimus ruber*) and the White Ibis (*Eudocimus albus*) in Venezuela. *Colonial Waterbirds* 10, 111-114. DOI: 10.2307/1521240

Ramos-Robles, M., Andresen, E. & Cecilia Diaz-Castelazo (2016) Temporal changes in the structure of a plant-frugivore network are influenced by bird migration and fruit availability. *PeerJ* 4, e2048. DOI: 10.7717/peerj.2048

Ratcliffe, N., Monteiro, L.R. & Hazevoet, C.J. (1999) Status of Raso Lark *Alauda razae* with notes on threats and foraging behaviour. *Bird Conservation International* 9, 43–46. DOI: unavailable

Recher, H. F. & Holmes, R. T. (2000) The foraging ecology of birds of eucalypt forest and woodland. I. Differences between males and females. *EMU* 100, 205–215. DOI: 10.1071/MU9904

Riegert, J., Fainová, D., Antczak, M., Sedláček, O., Reif, J., Pešata, M., (2011) Food niche differentiation in two syntopic sunbird species: a case study from the Cameroon Mountains. *Journal for Ornithology*, 152, 819-825. DOI: 10.1007/s10336-011-0650-0

Ripley, S. D. (1959) Competition between sunbird and honeyeater species in the Moluccan Islands. *The American Naturalist* 93, 127-132. DOI: 10.1086/282064

Robertson, O. J., McAlpine C., House, A. & Maron, M. (2013) Influence of interspecific competition and landscape structure on spatial homogenization of avian assemblages. *PLoS One* 8, e65299. DOI: 10.1371/journal.pone.0065299

Robinson, B.W. & Wilson, D.S. (1998) Optimal foraging, specialization, and a solution to Liem's paradox. *The American Naturalist* 151, 3–35. DOI: 10.1086/286113

Rodríguez, R. A., Herrera, A. M., Santander, J., Miranda, V. M., Fernández-Rodríguez, M. J., Quirós, Á., Reira, R., Frernández-Palacios, J. M., Otto, R., Escudero, C. G., Jiménez-Rodríguez, A., Navarro-Cerillo, R., Perdomo, M. E., Delgado, J. D., (2015) Uncertainty principle in niche assessment: A solution to the dilemma redundancy vs. competitive exclusion, and some analytical consequences. *Ecological Modeling* 316, 87-110. DOI: 10.1016/j.ecolmodel.2015.07.032

Root, R. B. (1967) The niche exploitation pattern of the bluegray gnatcatcher. *Ecological Monographs* 37, 317-350. DOI: 10.2307/1942327

Salisbury, C. L., Seddon, N., Cooney, C. R. & Tobias, J. A. (2012) The latitudinal gradient in dispersal constraints: ecological specialisation drives diversification in tropical birds. *Ecology Letters* 15, 847–855. DOI: 10.1111/j.1461-0248.2012.01806.x

Sandlin, E. A. (2000) Cue use affects resource subdivision among three coexisting hummingbird species. *Behavioural Ecology* 11, 550-559. DOI: 10.1093/beheco/11.5.550

Simberloff, D. & Dayan, T. (1991) The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics* 22, 115-143. DOI: 10.1146/annurev.es.22.110191.000555

Slater, P. J. (1994) Niche overlap between three sympatric, short-billed honeyeaters in Tasmania. *EMU* 94, 186-192. DOI: 10.1071/MU9940186

Stevens, G. C. (1989) The latitudinal gradient in geographical range – how so many species coexist in the tropics. *The American Naturalist* 133, 240-256. DOI: 10.1086/284913

Terborgh, J. (1971) Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology* 52(1), 23-40. DOI: 10.2307/1934735

Terborgh, J. W. & Faarborg, J. (1980) Saturation of bird communities in the West Indies. *The American Naturalist* 116, 178-195. DOI: 10.186/283621

Terborgh, J. & Weske, J. S. (1975) The role of competition in the distribution of Andean birds. *Ecology* 56, 562-576. DOI: 10.2307/1935491

Townsend Peterson, A. & Holt, R. D. (2003) Niche differentiation in Mexican birds: using point occurrences to detect ecological innovation. *Ecology Letters* 6, 774-782. DOI: 10.1046/j.1461-0248.2003.00502.x

Toyama, M. & Saitoh, T. (2011) Food-niche differences between two syntopic scops-owls on Okinawa Island, Japan. *Journal of Raptor Research* 45, 79-87. DOI: 10.3356/JRR-09-82.1

Walker, J. S. (2006) Resource use and rarity among frugivorous birds in a tropical rain forest on Sulawesi. *Biological Conservation* 130, 60-69. DOI: 10.1016/j.biocon.2005.12.002

Wallace, A.R. (1869) The Malay Archipelago, 1986 edition. Oxford University Press, Oxford.

Weinstein, B. G. & Graham, C. H. (2016) Evaluating broad scale patterns among related species using resource experiments in tropical hummingbirds. *Ecology* 97, 2086-2093. DOI: 10.1890/15-0328.1.

Whittaker, R. H., Levin, S. A. & Root, R. B. (1973) Niche, habitat, and ecotope. The American *Naturalist* 107, 321-338. DOI: 10.1086/282837

Whittingham, M.J., Butler, S.J., Quinn, J.L. & Cresswell, W. (2004) The effect of limited visibility on vigilance behaviour and speed of predator detection: implications for the conservation of granivorous passerines. *Oikos* 106, 377–385. DOI: 10.1111/j.0030-1299.2004.13132.x

*Van Wieringen, M. & Brouwer, K. (1990) Morphology and ecology of Scarlet (*Eudocimus ruber*) and White Ibis (*E. albus*): a comparative review. Pp. 7-15 in The Scarlet Ibis (*Eudocimus ruber*): status, conservation and recent research (P. C. Frederick, L. G. Morales, A. L. Spaans, and C. S. Luthin, eds.) International Waterfowl and Wetlands Research Bureau, Slimbridge, England

Wolf, L.L., Stiles, F.G. & Hainsworth, F.R. (1976) Ecological organization of a highland tropical hummingbird community. *Journal of Animal Ecology* 45, 349-379. DOI: 10.2307/3879

Wright, J.S. (2002). Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130, 1–14. DOI: 10.1007/s004420100809

Wright, J. & Radford, A. N. (2010) Variance-sensitive Green Woodhoopoes: a new explanation for sex differences in foraging? *Ethology* 116, 941-950. DOI: 10.1111/j.1439-0310.2010.01811.x

*secondary citation